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State-dependent cognition and its relevance to cultural evolution

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Abstract

Individuals cope with their worlds by using information. In humans in particular, an important potential source of information is cultural tradition. Evolutionary models have examined when it is advantageous to use cultural information, and psychological studies have examined the cognitive biases and priorities that may transform cultural traditions over time. However, these studies have not generally incorporated the idea that individuals vary in state. I argue that variation in state is likely to influence the relative payoffs of using cultural information versus gathering personal information; and also that people in different states will have different cognitive biases and priorities, leading them to transform cultural information in different ways. I explore hunger as one example of state variable likely to have consequences for cultural evolution. Variation in state has the potential to explain why cultural traditions and dynamics are so variable between individuals and populations. It offers evolutionarily-grounded links between the ecology in which individuals live, individual-level cognitive processes, and patterns of culture. However, incorporating heterogeneity of state also makes the modelling of cultural evolution more complex, particularly if the distribution of states is itself influenced by the distribution of cultural beliefs and practices.

Keywords: cultural evolution; social learning; cultural attraction; state-dependence; hunger

1. Introduction

Individuals cope with their worlds by making use of information, information being defined as a reduction in uncertainty about future events. There are multiple sources of such information. The genotype embodies information about recurrent properties and outcomes over the long time scale of many generations, as a consequence of the selective retention of genetic variants producing phenotypic 'fit' between behaviour and environment; in other words, because of natural selection. Experience over the individual's lifetime is another source of information; through processes of learning and inference, individuals can adjust their behaviour and cognition to local contingencies. And in some species, most notably in humans, there is a further potential source of information: cultural traditions. These offer information that embodies the results of other individuals' plasticity. For example, if I learn how to extract a particular foodstuff by asking or observing how a conspecific does it, I exploit the information about the world generated by that individual's, or some earlier individuals', trial-and-error learning of the technique. Cultural traditions represent an information source that is in a sense intermediate between genetic information and that generated by exclusively personal learning, in that the information may accumulate more slowly than one individual lifetime, and yet faster than the slow process of genetic evolution (Henrich and McElreath, 2003).

There are a number of distinct theoretical literatures on cultural information use viewed from an evolutionary perspective (see e.g. Boyd and Richerson, 1985; Henrich, 2004; Henrich and McElreath, 2003; Mesoudi, 2016; Richerson and Boyd, 2005; Sperber, 1996, 1985). These deal with such questions as when it is advantageous to rely on cultural information and when it is not; the dynamics of cultural traditions; and with how cognitive and motivational factors influence the kinds of information that is retained. These literatures have often, for simplicity, assumed a rather undifferentiated view of individuals (Colleran, 2016 , p. 8). That is, the fitness payoffs to using cultural information are assumed to be definable without knowing anything more about the individual who is using it; or the cognitive and motivational factors affecting cultural transmission are assumed to be fixed parts of species-typical psychology, rather than factors that could vary both within and between individuals. In this paper, I argue for a greater emphasis, in theorising about cultural information use, on the state-dependence of optimal decision-making, and the fact that cognitive priorities should and do vary with state. I will argue that state-dependence has the potential to explain inter- and intra-individual variability in the use of cultural information, as well as, potentially, some of the marked inter-population variability in the contents of cultural traditions that persist in humans.

In sections 2 and 3, I will briefly introduce two bodies of literature relevant to the information in cultural traditions; respectively, that on the evolution of social learning, and that on content biases or psychological factors of attraction. In section 4, I will introduce the notion of state and discuss why it should be relevant to cultural information. In section 5, I will provide an example from the literature on hunger, suggesting ways that hunger could affect the use as well as the transmission of cultural information. Section 6 concludes with some suggestions for future research.

2. The evolution of social learning

When should individuals rely on cultural tradition, and when should they instead base their decisions solely on personal experience? An influential line of thought here is the 'costly information hypothesis' (Boyd and Richerson, 1985; Richerson and Boyd, 2005). Generally speaking, acquiring direct personal experience of possible behavioural alternatives is costly: it can take time and expose the individual to errors and failures until they acquire the appropriate information. By learning from others, individuals can avoid some of these costs. Effectively, they can act as information scroungers, relying on the primary information production done by others in the population. A drawback of scrounging information is that the information may not be up to date or locally appropriate. A classic theoretical model by Rogers (1988) (extended by Boyd and Richerson, 1995) showed that as the frequency of using cultural information rather than personal experience increases in the population, its value drops.

To see why, consider the case where all individuals in the population are entirely reliant on adopting cultural tradition in some problem domain. Here, there is no personal verification that the information in the tradition is in fact useful. It may have become outdated or superceded, or not be suitable for the present location. Thus, in a population with 100% reliance on cultural tradition, the information decays in fidelity, and the relative fitness advantage to a rare personal learner is always positive. By contrast, when there is no reliance on cultural tradition at all in the population, the advantage to a rare user of cultural information is considerable. The rest of the population is generating high-quality information, and that information can be readily scrounged.

The conclusion of such reasoning is that reliance on cultural information will be under frequency-dependent selection, stabilizing at neither universal reliance on personal information-gathering, nor universal uncritical acceptance of cultural information. The balance of personal and cultural learning at this equilibrium will depend on factors such as the variability of the environment (since this affects the expected value of cultural information that may have been generated at an earlier time or different place), and the cost of acquiring information personally (Boyd and Richerson, 1995; Rogers, 1988). At the equilibrium in these models, the amount of personal learning is much lower than would be efficient for the population's learning about the world. This is because there is effectively a social dilemma: it is in each individual's interests that there be good quality information, but individuals personally acquiring that information pay all of the cost of doing so, whilst others will be able to scrounge the benefits whilst avoiding the costs. Like other simple evolutionary models producing frequency-dependent dynamics and a mixture of strategies at equilibrium, these models do not specify how the mixture of strategies will actually be generated: whether at equilibrium there will be two types of individual using different pure strategies, or each individual will itself use a mixed strategy. If the latter, the models provide no reason the mix should be different for different individuals, or at different times.

There are more complex models that are in many respects more realistic. Here, rather than individuals opting for either cultural tradition or personal information-gathering, they do a combination of the two, using cultural tradition to inform the starting point for personal information search, and hence making information acquisition more efficient overall (Boyd and Richerson, 1995). These models have the strength of recognising that in humans, social learning does not just produce the same information as individual learning but more cheaply; it also leads to cumulative bodies of knowledge that could not have been generated by any one individual. These models again assume a mixture of reliance on personal and cultural information, but again are silent on whether that mixture will be the same for all individuals at all times. This issue is important in view of experimental and observational evidence showing that reliance on cultural information is in fact highly variable between individuals, and possibly between populations (Efferson et al., 2008; Kameda and Nakanishi, 2002; McElreath et al., 2005; Mesoudi, 2011; Mesoudi et al., 2016). There are several possible explanations for seeing such variation in empirical studies. It could amount to measurement error. It could reflect artificiality in the experimental set-ups used to capture information use. It could also, however, reflect something real about cultural information use that generalises to 'the wild'.

Theoretical models such as those of Rogers (1988) and Boyd and Richerson (1995) rely on writing down fitness costs, for example the cost of acquiring personal information, which are assumed to be fixed. That is, the cost of acquiring personal information may vary for different cases (e.g it might be different for mushroom picking and making a comfortable coat), but for a given case, it is assumed to be the same for each individual in the population. However, general theory from behavioural ecology suggests that this assumption is not warranted. We return to this issue and its potential implications in section 4.

3. Psychological factors of attraction: The content of cultural traditions

In addition to the literature on when individuals should rely on cultural information at all, there are extensive literatures exploring the idea that they may be selective in what, within the totality of available cultural information, they attend to, retain and submit. Cultural information, unlike genetic information, does not appear to be faithfully transmitted under most circumstances, but gradually transforms as a result of the processing biases and affinities of the human mind. These cognitive and motivational factors have been incorporated into theory as 'content biases' (Boyd and Richerson, 1985; Henrich and McElreath, 2003) or 'psychological factors of attraction' (Sperber, 1996). To take one example, several studies have suggested that negative information (information about possible hazards) is more likely to be retained in cultural tradition than positive information (Bebbington et al., 2015; Fessler et al., 2014; Walker and Blaine, 1991). This reflects the repeated operation within cultural transmission of a bias that has often been documented in individual cognitive processing: the preferential attention to, or weighting of, negatively-valenced over positively-valenced information (Baumeister et al., 2001). The negativity bias has been given an adaptive interpretation (Fessler et al., 2014; Nesse, 2005). An unattended hazard has potential to be worse for fitness than an unattended reward. For example, missing a foraging patch might lead to the loss of a few easily-available calories, but missing a nearby predator could mean death, so even if predators are relatively rare relative to foraging patches, they should be afforded greater priority. To translate this to the cultural information context: ignoring news of where others have been predated is a worse error than ignoring news of where others have found food.

The literatures on psychological factors of attraction have for the most part investigated supposedly universal species-typical principles of processing selectivity, such as the overall negativity bias just discussed. There are two problems with such a focus, one empirical and one theoretical. The first is that empirical studies document very substantial variability in negativity- or disgust-bias. The bias appears on average across the whole sample, but some individuals show it much less than others, or do not do so at all (Fessler et al., 2014). Just as there appears to be variation in whether people use cultural-traditional information at all, there appears to be variation in the extent to which they exhibit the supposedly species-typical processing biases. The second, more theoretical problem, is that if phenomena such as the negativity bias were completely general, then, unless some counteracting force was as work, cultural traditions would all converge on containing *only* information about hazards. This does not seem to be the case, as the great variety of contents in diverse cultural traditions attests.

In interim summary, the literatures on cultural evolution have a tendency to treat individuals as undifferentiated. That is, all individuals are assumed to have the same properties and interests, and hence, the assumption is made for theoretical or explanatory purposes that all humans, at all times, can be represented by a 'representative human'. There are a few exceptions to this 'representative human' assumption. For example, Kandler and Steele (2009) show that adoption dynamics of culturally transmitted traits are altered if there is individual variability in the capacity to adopt. Nonetheless, the 'representative human' assumption has been widely made. A parallel phenomenon occurs in macro-economics, where 'representative agent' models attempt to predict aggregate economic patterns by assuming that all decision-makers are identical (or that any differences between them disappear in the aggregate). 'Representative agent' models have the advantage of simple tractability. However, economists have also criticized them, and sought alternative approaches, on the grounds that the predicted equilibria and dynamics change once heterogeneity amongst agents is incorporated (Heathcote et al., 2009; Kirman, 1992). Likewise, predictions about population-level patterns of culture may be quite different once heterogeneity amongst members of the population is incorporated. As I will now argue, one way of beginning to incorporate heterogeneity is to incorporate into our thinking the idea what people do with information varies depending on their state.

4. 'State' and its relevance to decision making

The previous two sections have established that there are some general theoretical ideas available about when and how people should process cultural information; but there are also issues of variation to explain. Individuals vary in the extent to which they use cultural information; and individuals vary in the presence or degree of content biases. I will argue that such variation is not a puzzle. On the contrary, it is exactly what we ought to expect if we base our theorising about cultural information on the premise that individuals can vary in state. This section introduces the notion of state and explains why it should be important for decision-making in general, and specifically for the use of cultural information.

A basic assumption in evolutionary reasoning is that individuals will make decisions that, on average across relevant types of environment, promote fitness. This leads theorists to try to write down fitness costs or benefits of doing action A rather than action B. It might well be possible to define the cost of an action in the currency of calories, say, or hours of time. However, the translation of proximal currencies such as energy or time into the ultimate currency of fitness is not trivial. In fact, there are good reasons for thinking that there is no simple, unconditional mapping function.

For example, consider the decision whether to go out foraging, and thereby be exposed to potential predation, or to remain hidden. To compute the evolutionary costs and benefits of going or not going, one needs to know the value of 50 calories, and of being killed, in the currency of fitness. Fitness is, roughly speaking, the representation of an organism's descendants in the population at some point in time far into the future. To maximise fitness, then, an individual would have to maximise its reproductive value (Fisher, 1930). Reproductive value is the mathematical expectation of future reproductive success. It follows that the more fitness-promoting of our two decisions (forage or hide) is the one associated with greater reproductive value.

Consider the scenario where our individual is on the very brink of starvation. If it hides and foregoes the 50 calories, it will definitely die. Its reproductive value under the option of hiding is therefore zero. It follows that, even if the probability of being predated if it forages is very close to 100%, it should still forage. There is a small chance the predator will fail to spot it, it will gain 50 calories, and have some chance of surviving; its reproductive value under foraging is therefore slightly higher than zero. Even if the predator will definitely be lethal, the individual is technically indifferent between hiding and foraging from a fitness perspective: both give the same reproductive value, namely zero. Being predated actually carries no fitness cost in this scenario, since dying by predator is no worse for fitness than starving to death.

Now by contrast consider an individual that is currently well fed, with considerable energetic reserves. It will definitely not starve to death within the next 24 hours. Not obtaining 50 immediate calories is thus of little consequence—perhaps no consequence at all—to its reproductive value. On the other hand, even a very small chance of being predated would make its reproductive value much lower if it forages. Thus, the respective fitness costs and benefits of being predated and 50 calories are quite different than for the starving individual. As a consequence, the well-fed individual should set a quite different threshold for when to forage under the risk of predation than the starving individual should (Trimmer et al., 2017). This explains the common observation that very hungry animals will come uncharacteristically close to humans to in order to forage.

The lesson of this example is that one should not simply assume costs and benefits for a given action that can be represented as single fixed numbers in some notional fitness currency. Fitness costs and benefits in fact arise from comparison of the reproductive values associated with different courses of action; and these in turn depend on what state the individual is in at the time of making the decision. By state, here, I mean measurable variables that characterise an individual, reflect its history, and have an impact on its reproductive value under different outcomes. Classic examples of state variables, as well as level of energetic reserves, could be toxin or pathogen load, temperature, size, or social rank.

This means that the term 'state', as I am using it here, encompasses both variables that can fluctuate reversibly over very short timescales, such as energy reserves or fatigue, and variables that tend to endure for most of a lifetime, such as size. Confusingly, in psychology, 'state' tends to be reserved for the reversible fluctuating states, whilst 'trait' is used to describe the life-long ones (see e.g. Fridhandler, 1986). My usage of 'state' follows that customary in behavioural ecology (e.g. Houston and McNamara, 1999) in encompassing both types of variation. Under this conception, traits are just enduring, and possibly irreversible, states.

Behavioural ecologists have recognised for some time that whether animals should, for example, prefer smaller-sooner over larger-later food sources, or food sources with fixed versus variable food amounts, depends on their state (Houston and McNamara, 1999; McNamara and Houston, 1992; Stephens, 1981). In other words, if we take an evolutionary perspective, our expectation should be not so much that, species-typically, individuals will have a bias for doing X over doing Y, but rather that decision-making should often be state-dependent. Individuals should modulate the decisions they make according to the current value of relevant state variables such as their strength, size, skill, fatigue or energetic reserves. There will thus be variation between individuals in which option they prefer (because populations contain individual variation in both immediate and enduring aspects of state), and there may also be variation within individuals over time (as aspects of their state fluctuate).

Now let us return to the issues concerning cultural information. First, consider Rogers' (1988) model of when to rely on cultural information rather than one's own personal experience. A critical variable in the model is the cost of individual learning: other things being equal, the higher this cost, the better the payoff for using cultural information. For any particular case, this cost is assumed in the model to be a fixed amount of fitness. But what the cost is supposed to represent biologically is the time and energy required to gather information in the domain for oneself. For a person free of disease and with abundant energetic reserves, the effective cost of personal information-gathering might be small (that is, more exactly, the reproductive value assuming the person gathers information personally is high). For a person with little spare energy or weak ability to perform the necessary observations herself, reproductive value if she tries to learn from her own experience might be zero. She won't get there on her own in the timescale she has available to her. The cost of individual learning for this person would therefore be very large. In other words, the model really should incorporate the fact that people vary in state; and whether people use cultural information or not should depend on their states as well as the already-documented factors described in section 2.

Proper explicit models are required here: one of the lessons of state-dependent theory is that the results of models are not always what one would intuitively expect (Houston and McNamara, 1999). Nonetheless, the intuitive prediction would be that when people's states are 'poor' (i.e. limited energy or strength available), they should make more use of cultural information, and as people's states get better, they should shift towards more personal information-gathering. A couple of recent examples could be interpreted in this light. Gopnik et al. (2017) suggested that people from resource-poor childhood environments might be less flexible learners as adults than those from resource-rich childhood environments. This could be interpreted in terms of an enduringly poorer adult state arising from a certain type of developmental history. van Schaik et al. (2016) have recently argued that whilst wild orangutans are highly dependent on social learning and do not tend to innovate, orangutans in zoos and sanctuaries innovate at a much higher rate. They suggest that the benign conditions of captivity result in individuals being in a state where the costs of innovation are much reduced. Examples such as these suggest we should move away from characterising a species as having a fixed capacity or propensity to innovate or to learn socially, in favour of understanding that these behaviours may change according to the states of the individuals we happen to be studying.

I have discussed state variation thus far as possibly shifting individuals from individual learning to using cultural information, or vice versa. However, equally plausible is the possibility that state could affect learning strategies *within* cultural information acquisition. For example, adopting the most

widespread practice in one's social network (conformist learning) might carry a different combination of riskiness and difficulty than attempting to emulate the most apparently successful members of one's social network (prestige-biased learning). The simple dichotomy of individual versus social learning, whilst useful as an analytical convenience, is somewhat artificial. Thus, more generally, it is plausible to argue that individual variation in state variables could affect optimal and actual strategies for acquiring information from the large set of possible ways that an individual could do this.

State might also plausibly affect psychological processing biases. Arguments for the adaptive basis of negativity bias are based on the respective sizes of the fitness costs of missing the information of the two types, putatively very large for a missed hazard, and smaller for a missed reward (Fessler et al., 2014; Nesse, 2005). However, these benefits and costs, on the scale of fitness, cannot be precisely defined without knowing an individual's state (Bateson et al., 2011). For example, for an individual currently able to run fast, a nearby predator might not much reduce reproductive value; she can simply run away if attacked. For her, the difference between the fitness cost of an unattended predator and the fitness cost of an unattended food source might be modest. She should perhaps be equally attentive to cues of reward and those of hazard. For an individual who is currently lame, a nearby predator is a disaster, since she cannot escape it. Her information-processing bias should be for cues of hazard at the expense of cues of reward. Thus, we should expect the magnitude of any negativity-bias in cognition to be state-dependent. There is some evidence in favour of this view. For example, anxiety (which can be roughly equated to the presence of negativity biases in information processing) is variable between individuals, variable over time within individuals, and strongly linked to physical health and robustness (Bateson et al., 2011).

To apply this to cultural information use, we should therefore expect people who have limited ability to cope with hazards to be particularly attentive to culturally-available information about hazards of that kind. Subcultures in which many of the individual people are in such states would therefore preferentially retain and transmit hazard-related information, compared to subcultures in which few people are in such states. Over time, the cultural traditions of networks of people with, on average, low ability to cope with hazards would come to look very different from the cultural traditions of networks of people with, on average, high ability to cope, due to the repeated action of successive individuals' processing biases. Whilst previous studies have acknowledged that there is likely to be variation in the extent of negativity bias (Fessler et al., 2014), and that individual differences in anxiety might be relevant (Bebbington et al., 2015), the idea that networks of people with different distributions of states might produce systematically different cultural traditions has not been thoroughly explored.

To summarise, theoretical predictions about when individuals should prefer to use cultural rather than personal information should take into account the fact there may be variation in state, and state may well influence the effective fitness costs and benefits associated with different strategies or biases. There may be many different relevant state variables (energetic reserves, learning abilities, physical strength), and each of these could have different influences for different problem domains. Thus, it will be necessary to construct more biologically realistic models of cultural information use, that take into account what kinds of things the information is being used for, and what aspects of state could affect the fitness payoffs for different courses of action. These models could show that whether people use cultural information, and how that cultural information evolves, can shift dramatically without any change in the genetic makeup of the population, according to the distribution of biological states of the agents. I will now discuss one case study of how a state variable could be included into the research programme of social learning and cultural evolution, namely the state variable hunger.

5. State influences cognition and has implications for culture: The example of hunger

Hunger is an internal psychological variable that informs the individual of its future energetic status. Humans and other animals generally defend a body weight set point, reflecting the balance between metabolic and locomotor costs, and sufficient fat as a buffer or store for reproduction (Nettle et al., 2017; Speakman et al., 2011). Hunger represents a graded internal signal that food intake is required to maintain the set point; food must be found, captured and ingested soon.

Evidence from across species shows that hunger (operationalised in what follows either by self-report, or by food deprivation, energy reserves, or blood glucose) changes a whole suite of cognitive and motivational variables. These reflect the function of hunger in fairly obvious ways. Hungry humans think a lot about food (Keys et al., 1950); show attentional biases towards cues of food in their environments (Tapper et al., 2010); show an increased motivation to work for food, and lose the desire to work for, and ability to concentrate on, non-food stimuli (Orquin and Kurzban, 2016). Hunger increases impulsivity in both humans and non-human animals: that is, the subjective value of a small-but-soon reward relative to a larger-but-later reward increases as the individual becomes hungrier (Bateson et al., 2015; Orquin and Kurzban, 2016). In humans, there is evidence that the impulsivity spills over into decisions made in problem domains other than food, such as those involving money (Wang and Dvorak, 2010). Hungry individuals are also more aggressive (see Nettle, 2017). In starlings, hungry individuals become less discriminating in what they are prepared to eat (Bloxham et al., 2014). In humans, there is evidence that hungry humans shift away from deliberative decision-making (i.e. accurate but effortful styles of decision making based on extensive consideration of relevant information), towards more heuristic decision making (simple, rapid rules producing less accurate decisions; Danziger et al., 2011; Masicampo and Baumeister, 2015; McMahon and Scheel-Carroll, 2010). In summary, the effect of hunger is to shift organismal priorities towards getting some food soon and cheaply, even if it is not the optimal resource, and even at the expense of other activities. This shift should not be conceptualized as mere 'bad performance'. On the contrary, it may reflect an evolved capacity to respond adaptively to variation in one's current state.

What then might be the effect of hunger on the use and transmission of cultural information? The costly information hypothesis and the models associated with it conceptualise the choice of whether to use cultural information or whether to gather information personally as a choice between information that is quick and easy to get, but possibly not very accurate (cultural information); and information which is long and effortful to obtain but of higher quality in the end (personally-gathered information). From the review of the effects of hunger in the previous paragraph, the prediction seems obvious. Hungry people will be more prepared to use cultural information—in effect, to copy what everyone else is doing—whereas people who are not hungry will be prepared to undertake costly personal information foraging. There is no direct experimental evidence relevant to this prediction, though there are some somewhat related findings from the animal literature on contrafreeloading (Osborne, 1977). Contrafreeloading refers to working to obtain a food that is available more cheaply elsewhere. For example, digging up buried food whilst the same food is available on the surface would constitute contrafreeloading. In violation of simple micro-economic principles, animals of many species will contrafreeload some of the time when offered the choice. The general interpretation is that they are devoting some of their energy to foraging for information—the harder-to-access source may be better in some way, or may be valuable in the future when the easy source depletes (Bean et al., 1999). Thus, contrafreeloading is somewhat akin to doing costly personal information gathering when one could simply copy what others are doing. And a consistent finding in the contrafreeloading literature is that individuals contrafreeload less when they are hungry (Inglis and Ferguson, 1986): the relative fitness payoffs to getting some calories now, versus having better information about the world, are shifted by a change in state.

We can make a first set of predictions about what we should expect to happen in terms of a punctuated episode of cultural information use or cultural transmission. Other things being equal,

when given the choice, currently hungry individuals should be expected to make greater use of cultural information, whilst currently more sated individuals will be prepared to expend more effort on personal information search. Since hungry people have attentional and memorial biases towards food-related information, and decreased motivation for other kinds of information, we should expect that the food-related aspects of a cultural representation would be differentially retained and transmitted compared to the other aspects when transmitted by someone currently hungry than someone currently sated. These predictions are eminently testable, and hunger has the particular advantage that it can be very effectively manipulated experimentally. There are experimental paradigms that assess people's willingness to use cultural information (copying what others do), versus personal information search, in laboratory tasks (McElreath et al., 2005; Mesoudi, 2011). Studies using such paradigms have documented substantial variability in cultural information use, but not measured or manipulated state variables such as hunger that might explain some of this variability. An interesting question here is whether any hunger effects would be specific to choosing or searching for foods, or whether, as in the case of impulsivity, hunger effects might bleed out into non-food decisions (Wang and Dvorak, 2010). As for predictions concerning the effect of hunger on selective transmission of cultural information, the method of serial reproduction—where each individual in a chain is exposed to and reproduces a complex set of information—has been widely used to examine the cumulative effect of processing biases (e.g. Bebbington et al., 2015). These methods could be readily applied with participants differing in their level of hunger.

Given that hunger is a transient state, it is not obvious that hunger-induced variation in information use will have any important consequence for cultural evolution at the population level. Any biases introduced by people when they are hungry may be diluted out in subsequent transmission by people who are not currently hungry. However, societies living in different environments experience very different schedules of hunger. For example, famine and food insecurity are rare in some societies, and endemic in others. Within societies, there is variation in the experience of hunger, notably between the rich and the poor. Even in affluent societies, widely supposed to suffer from diseases of affluence and excess, involuntary hunger is actually surprisingly widespread amongst the poorest sector of the population (Gundersen et al., 2011; Nettle, 2017). Thus, different distributions of hunger have the potential to explain aspects of the observed variability in human cultural traditions. If currently hungry people shift towards more uncritical use of cultural information and away from personal information gathering, then the traditions of societies or subcultures in which many of the people are hungry at any given time, should be more stable, more conformist, and less innovative than those in which few of the people are hungry at any given time. We should expect that the vernacular traditions of societies that collectively experience extensive hunger should contain more food-related content, and content about the satisfaction of immediate need, than the traditions of societies where hunger is rare. These effects will be particularly likely to be visible if, as has been suggested, frequent exposure to hunger over the life course leaves a psychological residue, so that individuals continue to behave as if currently hungry even when they are not (Bloxham et al., 2014; Olson et al., 2007).

The kinds of predictions described above would be testable with cultural traditions as the unit of analysis. Comparative ethnographic resources such as the Human Relations Area Files and Standard Cross-Cultural Sample summarise cultural contents in various areas (folklore, religion, morality), as well as details on the food ecology, for many different traditional societies. There is thus potential for comparative analyses of associations between endemicity of hunger and the content of cultural traditions (see Cashdan and Steele, 2013; Murray et al., 2017; Roes and Raymond, 2003 for exemplars of the kinds of analyses that are possible using this material).

In short, the state of hunger has explanatory potential for the apparent variability in the use and content of cultural traditions, both at the micro-level of individual decision making, and potentially at the macro-level of features of the cultural traditions of different social groups, given that different social groups have different distributions of exposure to hunger. This exemplifies how the notion of

state has the potential to link the micro-level of individual cognition to the macro-level of the stability and persistence of human cultural traditions.

6. Conclusions and suggestions for future research

In this paper, I have suggested that models of human reliance on cultural information should incorporate the idea that individuals vary in state; that the fitness costs and benefits of different information-use strategies are likely to be state dependent; and that the variable cognitive priorities and biases associated with different states are likely to influence the direction of cultural evolution. These principles offer an avenue of explanation for why people vary so much in how they use and transform cultural information. Taking account of state variation would bring greater biological realism into the literature on cultural information, and has the potential to better integrate it with the study of development and aging. Although there has been some consideration of the effects of age-structure on cultural dynamics (Fogarty et al., 2013), chronological age itself is often not the most useful explanatory variable. The reasons that individuals of different chronological ages behave in different ways are often more deeply explained in terms of changes over time in state variables, such as strength, size, or accumulated somatic damage (Andrews et al., 2017; McNamara and Houston, 1996). Moreover, effects of developmental experience on adult phenotype can often be explained in terms of the developmental experience lastingly altering adult state variables (Nettle and Bateson, 2015; Rickard et al., 2014).

State-dependence of information use seems to offer both the promise of clear causal explanations for patterns of culture, and a worry that such explanations may not be forthcoming. On the promise side, the concept of state offers a potentially important causal bridge between the ecological context in which people operate (e.g. the food regime or dangerousness of the environment), their individual psychology (e.g. motivational variables and cognitive biases), and cultural phenomena. Studying this bridge seems straightforward, though it may not be easy in practice. Even assuming we can measure state variables and cultural traditions in real human populations, causal decomposition will be difficult. There are numerous potential state variables to consider, and the occurrence of these will not be independent. The literatures linking pathogen prevalence to patterns of behaviour (Nettle, 2009; Pollet et al., 2014), or adoption dynamics to individual learning strategies (Hoppitt et al., 2010; Kandler and Steele, 2009), serve to illustrate some of the inferential problems that can be involved in trying to infer individual causal mechanisms from correlational data. More positively, some state variables might fluctuate acutely and/or can be manipulated experimentally, as I argued for the case of hunger in section 5. This opens the way for stronger tests, at least at in small groups or experimental micro-societies, of their causal impact on patterns of culture.

On the worry side, making 'representative human' assumptions makes it possible to model population-level patterns of culture tractably. Once heterogeneity of individuals is introduced, via a distribution of states, analysis will become less tractable, and population-level cultural consequences are likely to be more complex and difficult to generalize about (Page, 2015). For example, we have no idea whether the culture of a population in which all individuals are anxious 10% of the time evolves differently from one in which 10% of individuals are anxious all of the time. The complexity will be particularly great if state is endogenized. That is, not only is there a distribution of states across the individuals in the population, but that distribution is itself changed by the cultural beliefs and practices individuals are currently employing. The dynamics and equilibria in such a case are hard to predict in general. Thus, this paper has offered only a promissory introduction to the potential relevance of state. Whether state turns out to add explanatory power to our analysis of culture, to make explanation more difficult, or make no difference, will depend on future detailed theoretical and empirical investigations.

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